THE BATRACHIA OF THE PERMIAN PERIOD OF NORTH AMERICA.

BY E. D. COPE.

THE class Batrachia holds an important position in the history of the Vertebrata, as the first member of that kingdom which occupied the land on the advent of the conditions suitable for air-breathing types. It thus stands in ancestral relation to the lines of the Sauropsida and Mammalia, and as the immediate descendant of the fishes.

There are several orders of Batrachia, and they display remarkable diversities of skeletal structure. For the better understanding of these, I give the following table of their principal definitions :[1]

I. Supraoccipital, intercalary and supratemporal bones present. Propodial bones distinct.

Vertebral centra, including atlas, segmented, one set of segments together supporting one arch ..... *Rhachitomi.*

Vertebræ segmented, the superior and inferior segments each complete, forming two centra to each arch. ..... *Embolomeri*

Vertebral centra, including atlas, not segmented; one to each arch.... *Stegocephali.*

II. Supraoccipital and supratemporal bones wanting. Frontal and propodial bones distinct.

a An os intercalare.

A palatine arch and separate caudal vertebræ..... *Proteida.*

aa No os intercalare.

A maxillary arch; palatine arch imperfect; nasals, premaxillaries and caudal vertebræ distinct ..... *Urodela.*

Maxillary and palatine arches distinct; nasals and premaxillaries united *Gymnophiona.*

No maxillary or palatine arches; nasals and premaxillary, also caudal vertebræ, distinct ..... *Trachystomata.*

III. Supraoccipital, intercalare and supratemporal bones wanting. Frontals and parietals connate; propodial bones and caudal vertebræ confluent.

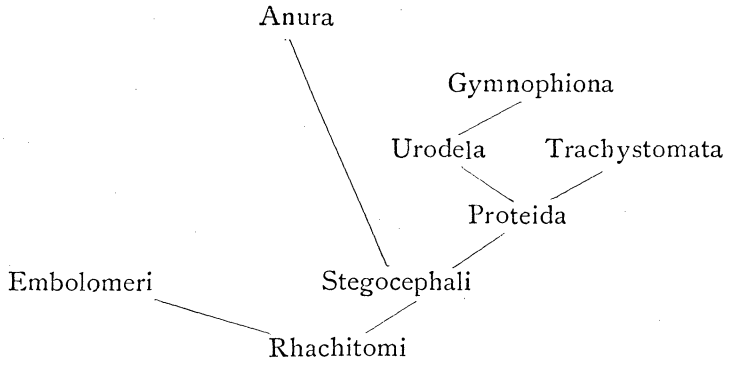
Premaxillaries distinct from nasals; no palatine arch; astragalus and calcaneum elongate, forming a distinct segment of the limb..... *Anura.*

The animals of the division I are all extinct. Division II includes the salamanders and their allies, with the worm-like Cœcilians (Gymnophiona); while the third division embraces the frogs, toads, etc.

[1] This is partly derived from the table which I have given in Vol. II Palæontology of the Geological Survey of Ohio, 1874, p. 352. See also Proceedings Philadelphia Academy, 1868, p. 211.

The characters displayed by the three divisions in question, indicate their relationships to be as follows: The orders of division 1 present in their cranial structure a greater resemblance to the limb-finned or crossopterygian fishes, than do either of the others. The third division is the most divergent from that type, and is in various respects the most specialized. This specialization consists not only in a departure from the primitive Batrachia, but also from all other forms of Vertebrata. Its specialization is seen in the loss and coössification of various parts of the skeleton. The Urodela display characters intermediate between the extremes of the class. Near them the Trachystomata (Sirenidæ) are inferior by loss of parts of the skull, and of the pelvic arch, the result, probably, of a process of degeneration. The same is probably true of the Proteida, which have lost the maxillary arch of the Stegocephali, but retain their os intercalare.[1]

As regards the extinct orders, the primitive type is evidently the Rhachitomi, whose vertebral column displays an arrest of characters which are transitional in the higher Vertebrata. From this group the orders Embolomeri and Stegocephali have evidently been derived. We may then present the following genealogical table of the class Batrachia:



As regards the connection of the class, as a whole, with other classes of Vertebrata, it is very probable that the extinct orders, as the Rhachitomi, were derived from some extinct form of Dipnoan fishes more or less related to the group of which the genus Ceratodus is a representative. In this type we have a persistent chorda dorsalis; fins which present the type from which ambulatory

[1] Of Cuvier; Epiotic of Huxley, according to Vrolik.

limbs were derived; a pelvis; and a cranium nearer that of the batrachians than most other fishes present. The Crossopterygia are a little on one side of the parental stem, since they have no pelvis, and their limbs begin to show a beginning of that reduction and specialization, which is carried to such an extent in the Actinopteri, or typical fishes.

The Batrachia are supposed by Professor Huxley to have given origin to the Mammalia. There are many reasons to sustain this view, nevertheless no progress has yet been made by palæontological research in filling up the great interval which separates the Permian Batrachia from the Mesozoic Mammalia. It is also true that the limb bones of the Permian Reptilian order of the Theromorpha more nearly resemble those of the lowest Mammalia, the Monotremata, than do those of any other known forms.

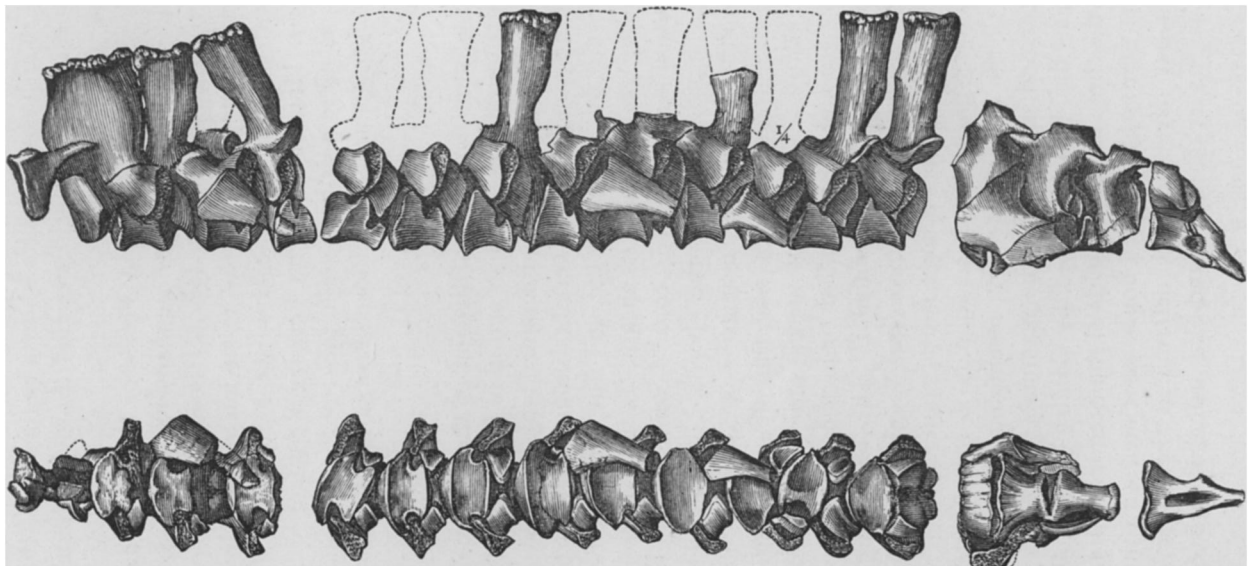
The Rachitomi.

I proposed this name[1] for a division of the Batrachia which predominated during the Permian period in both the old and new worlds. As stated above in the differential table, it is characterized by the primitive condition of its vertebral column. The cartilaginous chorda dorsalis was present in life, and the vertebral bodies are represented by ossifications of its sheath. In the Trimerorhachidæ this ossification is superficial or cortical, while in the Eryopidæ it penetrated more deeply into the chorda. The segments of the centrum are three in number, an inferior one or intercentrum, and a superior lateral one on each side, the pleurocentrum, as it is called by Gaudry. The lateral pieces support the neural arch, and on this account I have called them the centrum proper, as distinguished from the intercentrum. The neural arch is unbroken, and displays articular processes (zygapophyses) of usual form, and in some genera a large neural spine.

The shoulder-girdle of these animals is remarkable for the small size of the coracoid element, resembling in this respect the salamanders, and approaching the mammals. There is probably a clavicle, as has been observed by Gaudry in Actinodon. He also finds the three thoracic shields of the Stegocephali (episterna and entosternum). I have such bones associated with the American forms, but have not yet determined their species. The humerus has no head, but a band-like articular surface instead.

[1] American Naturalist, 1882, p. 333.

PLATE II.



ERYOPS MEGACEPHALUS Cope. 1/4

Its condyles, when present, are, on the other hand, well developed, and resemble those of salamanders, and of certain Mesozoic and lowest Tertiary mammals, as Meniscoëssus of the Laramie, and Catopsalis of the Puerco. The terminal phalanges were not converted into claws, but were flat and obtuse, as in existing Batrachia.

The pelvic arch is intermediate between those of the Anura and salamanders, and resembled closely that of the Pelycosaurian division of the Theromorphous reptiles of the same age. The pubis and ischium are solidly united, without the intervention of an obturator foramen, and those of opposite sides form a boat-shaped body. This is suspended from the sacrum by a vertical ilium, which rises from near the middle of each side. Its proportions are about as in the salamanders. The femur has no head proper, and the distal condyles are better distinguished than in any other Batrachia and than in most Reptilia.

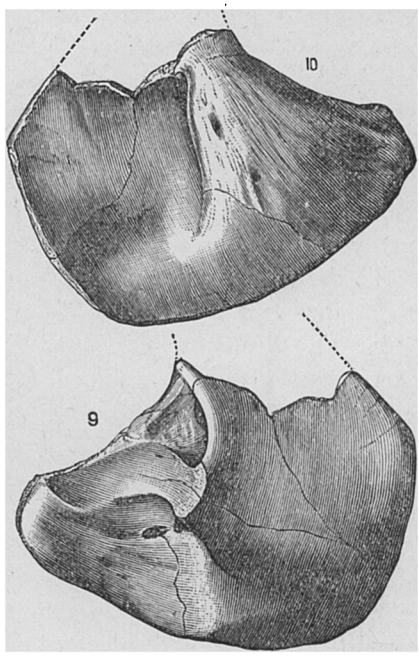


FIG. 1.—*Eryops megacephalus* Cope. Inferiol part of scapular arch of a different individuar from that represented in Pl. II; four-fifteenths nat. size. Upper figure from front; lower, posterior view.

The species of the Rachitomi are rather salamander-like in proportions, with relatively short legs and long tail, except in Eryops, where the latter was probably represented by a stump (see Plate II). They had relatively large heads with wide gape, as in the frogs. None of the known species can be supposed to have had powers of leaping as in those modern animals.

None of the known species had a formidable dentition, and in all of them the dentine is simply inflected, so that the section of a tooth presents a mass of closely-packed radii.

The two families of this order are well distinguished by the

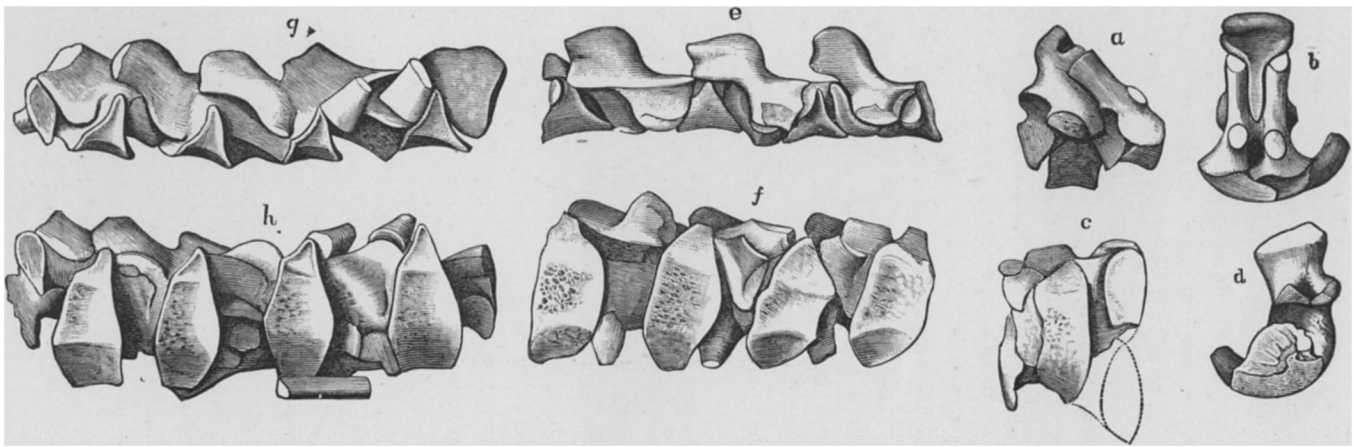
form of the basioccipital bone. In the Trimerorhachidæ its condyle is simple and concave, somewhat as in some fishes. The Eryopidæ have the two condyles characteristic of Batrachia generally. This difference might be esteemed as of greater than family significance, but it is less considerable than at first sight appears. The single cotylus-like basioccipital bone of the Trimerorhachidæ is notched above, sometimes deeply, to receive the apex of the notochord. A corresponding notch on the inferior edge would, if present, divide the articulation into two surfaces, which would greatly resemble the condyles of Eryops. The latter are flat and look partly towards each other, and are evidently separated originally by the *fissura notochordæ*.

To the Trimerorhachidæ I have referred, with certainty, only the genus Trimerorhachis. I have been unable to learn the structure of the vertebræ in the European genus Archegosaurus. According to some authors they are simple, as in the Stegocephali. Specimens of this kind, of the size of the *Archegosaurus decheni*, are found in the locality where the latter occurs, *i. e.*, Saarbrücken in Alsace; while rachitomous vertebræ from the same locality are of larger size, and resemble those of Eryops (Mus. Princeton, N. J.).

I have called attention to the structure of the vertebral column of the Rachitomi from a mechanical standpoint.[1] The notochord persists, the osseous elements about it in the sheath or skin, in the form of regular concave segments much like such segments as are cut from the skin of an orange, *i. e.*, parts of spheres, having greater or less thickness according to the group or species. Now the point of divergence of these segments is on the side of the column, the upper segments rising, and the lower segments expanding downwards. To the upper segments are attached the arches and their articulation, and the lower segments are like the segments of a sphere. If you take a flexible cylinder, covered with a more or less resistant skin or sheath, and bend that cylinder sidewise, you will of course find that the folds of the surface will take place along the line of the shortest curve, which is on the side; and, as a matter of fact, you will have breaks of very much the character of the sutures of these vertebral segments. It may not be so symmetrical as in the actual animal, for organic growth is symmetrical so far as not interfered with; for, when we have two

[1] *Science*, 1883, p. 276.

PLATE IV.



TRIMERORHACHIS INSIGNIS Cope. $\frac{1}{1}$

forces, the one of growth and the other of change or interruption, and they contend, we still have in the organic being a quite symmetrical result. In the cylinder bending in this way, of course the shortest line of curve is at the center of the side of the cylinder, and the longest curve is at the summit and base, and the shortest curve will be the point of fracture. And I presume it has happened in the case of the construction of the segments of the sheath of the vertebral column that the lateral motion of the animal swimming has been the actual cause of the disposition of the osseous material in this form.

A very good illustration of the effect of bending of a more or less flexible cylinder may be seen in the folds on the inner concave side of one's coat sleeve. In the accompanying figure the folds in the cloth represent the lines of flexure, or what would be

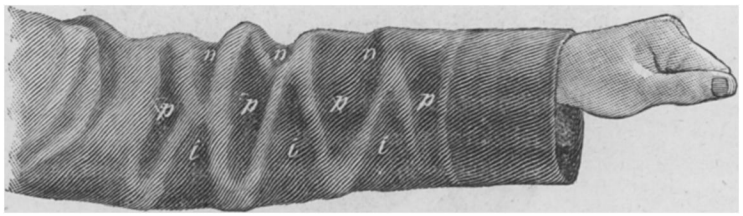


FIG. 2.—Sleeve of a coat, showing folds produced by lateral flexure, which leave interspaces similar to the segments of a rachitomous vertebra. Thus *i* represents intercentrum, *p*, pleurocentrum, and *n*, neurapophysis.

in a seat of ossific deposit, of interruption; while the interspaces represent the segments bounded by such lines. The correspondence with the segments of the vertebræ of the Rhachitomi is remarkable. At the base we have the wide lenticular intercentrum (viewed partly from below in the cut); between their lateral apices we have the pleurocentra, and above, another segment, which in the vertebra is the base of the neural arch.

The view that the segmentation of the vertebral column is the result of lateral alternating strains, was proposed by Herbert Spencer (Principles of Biology, II, p. 195). The present researches confirm this hypothesis in general. Mr. Spencer did not, however, specify the kind of segmentation to be expected from this process, and leaves it to be inferred that the segments will be cylinders of greater or less length. Thus he says (p. 205) "in a vertebral column of which the axis is beginning to ossify, the centrums consist of bony rings inclosing a still continuous rod of cartilage." And it is true that this is the primitive form in

embryology, but whether true in any instance in palæontological history yet remains to be ascertained.

TRIMERORHACHIS Cope.

This genus presents the most imperfect vertebræ known in the order. It differs from all others, including Archegosaurus, in the lack of a distinct neural spine. Its humeri do not display condyles, but had cartilaginous articular surfaces. The teeth are rather small

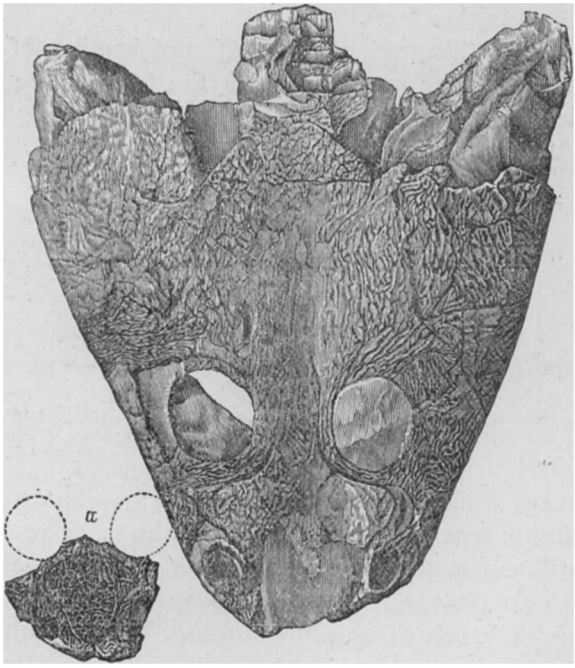


FIG. 3.—*Trimerorhachis insignis*, skull from above; one-half natural size. Smaller figure; muzzle showing sculpture and nares.

and of equal size, except a large one or two inside the external series near the anterior part of the mouth.

Two species are known, the *T. insignis* Cope, and *T. bilobatus* Cope, both from the Permian beds of Texas. Both were probably of slender proportions, and had short weak limbs.[1] The head of the *T. insignis* is wide, flat and rounded, and its superior surface is strongly wrinkled. The lyriform mucous groove does

[1] This proportion is not certainly known.

not extend behind the orbits. This was a very abundant species

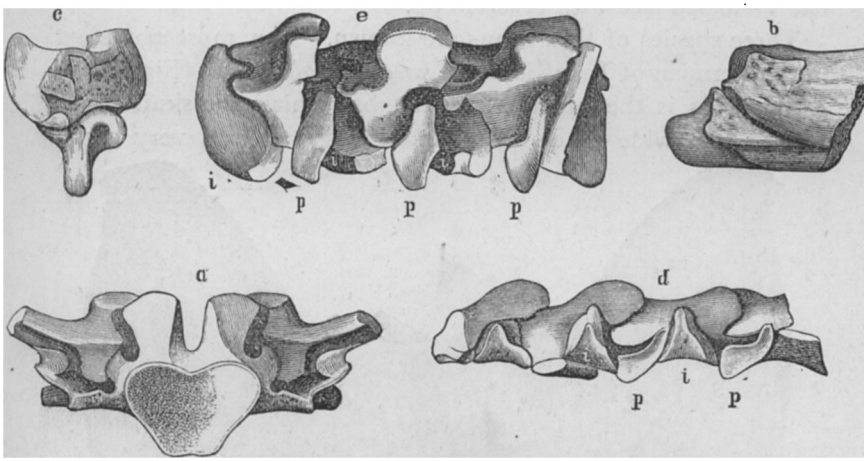


FIG. 4.—*Trimerorachis insignis* Cope; parts of skeleton, natural size. Fig. *a* basi-occipital, exoccipital and periotic bones, posterior view; *b*, angle of mandible, external view; *c*, the same, posterior view; *d*, part of vertebral column depressed by pressure, showing the intercentra (*i*) and the pleurocentra (*p*); *e*, a part of the vertebral column, oblique view, showing double neural arches and zygapophyses.

during the Permian period in Texas, and probably possessed aquatic habits.

ERYOPS Cope.

This genus is the best-known American representative of the Eryopidæ. This family includes also Acheloma, Anisodexis, and probably Zatrachys in America, and Actinodon in Europe. The last-named genus occurs in the Permian beds near Autun, in Central France, and has been well elucidated by the labors of Professor Gaudry of the Jardin des Plantes.

In Eryops the teeth are arranged much as in Trimerorhachis, in external series of nearly uniform size, with some large ones in the anterior parts of both jaws, a little within the external rows. As in that genus, the supra-temporal does not display a free external margin, as it does in Cricotus, and there is no angular process of the mandible. There is, on the other hand, no lyra. The intercentra and pleurocentra are much more robust than in Trimerorhachis. The neural spines of the vertebræ are large, and have expanded summits. The caudal vertebræ appear to have been very few, and to have been confluent into a short conical coccyx. The inferior elements of the pelvis are remarkably

heavy, the pubis being thickened in front, and truncated with a flat V-shaped face with reverted lip.

Three species of this genus are known. The most abundant in the Permian of Texas is the *E. megacephalus* Cope (Figs. 1 and 5–6). This is the largest American batrachian, the skull measuring a foot wide by eighteen inches long. It was very abun-

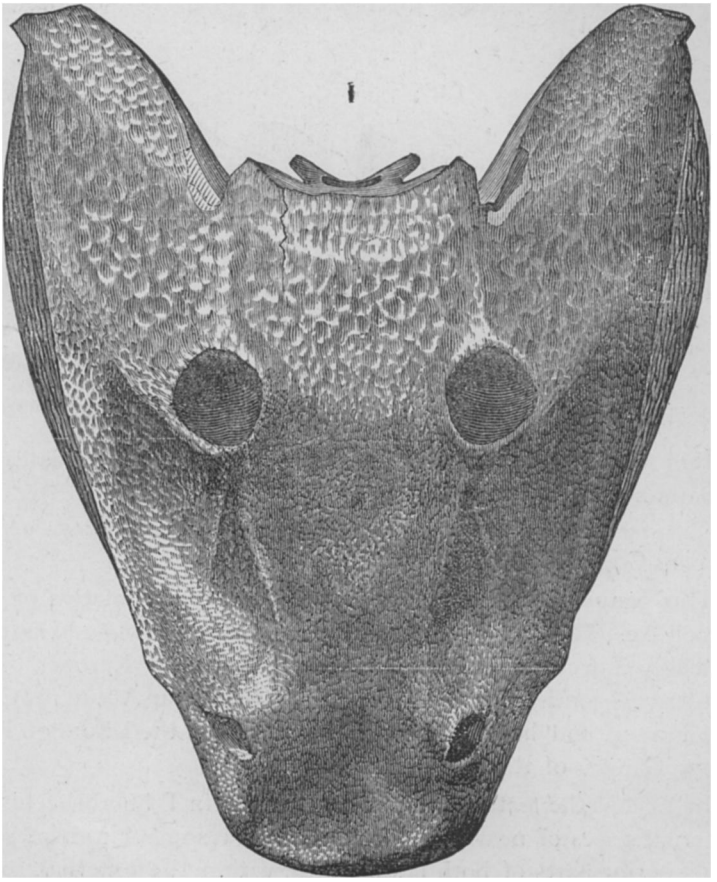
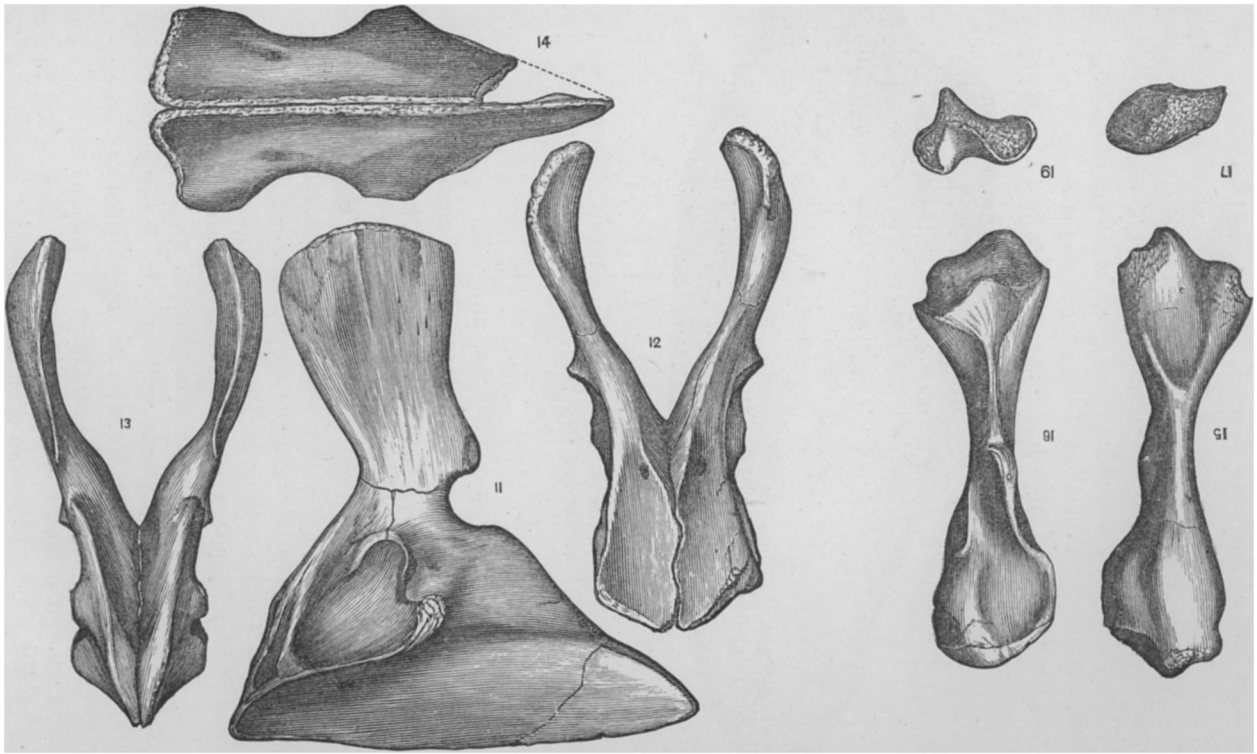


FIG. 5.—*Eryops megacephalus* Cope, skull from above, one-fifth nat. size.

dant, constituting with the reptilian genus Dimetrodon, the most prominent type of the Permian fauna in this country. The vertebral column is slender when compared with the size of the limbs, and especially of the head. The restoration of a species of European Labyrinthodon by Mr. Waterhouse Hawkins does not badly represent this species. The *E. reticulatus* Cope, is a much smaller species, and the sculpture of the skull is



ERYOPS MEGACEPHALUS Cope. $\frac{4}{15}$

sharper and of a net-like pattern. The neural spines are not so much expanded at the apex. It has been found in the Permian beds of New Mexico. The *E. ferricolus* Cope, is a still smaller species, known from skulls from Texas. This, with the *E. megacephalus* and the *Trimerorhachis insignis*, were found by Mr. Jacob Boll, a naturalist of Dallas, Texas, who was a man of many accomplishments and an ardent explorer. He lost his life through

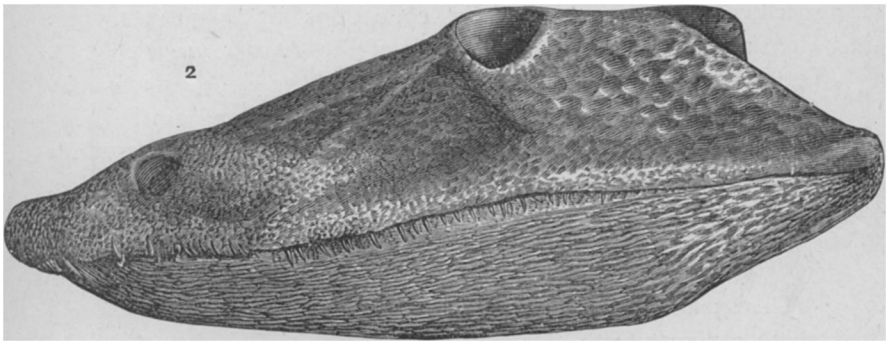


FIG. 6.—Side view of skull of *Eryops megacephalus*, one-fifth nat. size.

his indifference to his personal comfort while exploring the Permian beds at my instance.

ACHELOMA Cope.

This genus is allied to Eryops, and differs in two principal points. One of these is the absence of the lateral border of the cranial table formed by the external side of the *os intercalare* in Eryops and various other genera, the posterior outline of the skull being thus continuous. The other is the absence of the condyles of the humerus, a point in which it resembles Trimerorhachis. The vertebral segments are more robust than in Trimerorhachis, and less so than in Eryops; and it agrees with those genera in the absence of the mandibular angular process.

The only known species of this genus is the *A. cumminsi* from Texas. Its structure is pretty well known. It resembles in general the *Eryops megacephalus* with its small orbits and absence of lyrate groove, but is smaller and differs in various details. The skull is triangular, and measures a little more than seven inches long by five wide, and has an open honeycombed sculpture of the surface. The vertebræ and limbs are small for the size of the skull; and in the former the summits of the neural spine are not expanded.

ANISODEXIS Cope.

This genus differs from those previously described, in the inequality in the sizes of the teeth of the external series. Thus in the upper jaw there is a very large one in the position of a canine, and in the lower jaw there are some large ones near the symphysis. The neural arch of the vertebræ resembles that of the genus Acheloma. The *A. imbricarius* Cope, is the only known species, and is represented in collections by fragments only. The size of its skull is nearly that of the *Eryops megacephalus.* The sculpture of the superior surface of the skull is a coarse reticulation; that of the sides of the jaws is of an imbricate or shingle-like character. The limbs are unknown. The vertebræ do not exhibit an expansion of the summit of the neural spine. From the Texas beds.

ZATRACHYS Cope.

This genus was originally represented by a maxillary bone, which supports teeth of equal length, and whose surface is extraordinarily rugose. In the typical species, *Z. serratus*, the rugosities project in the form of teeth along the external alveolar border. Individuals with sculptured neural spines and dermal bones are referred here. The intercentra are much like those of Eryops and Acheloma.

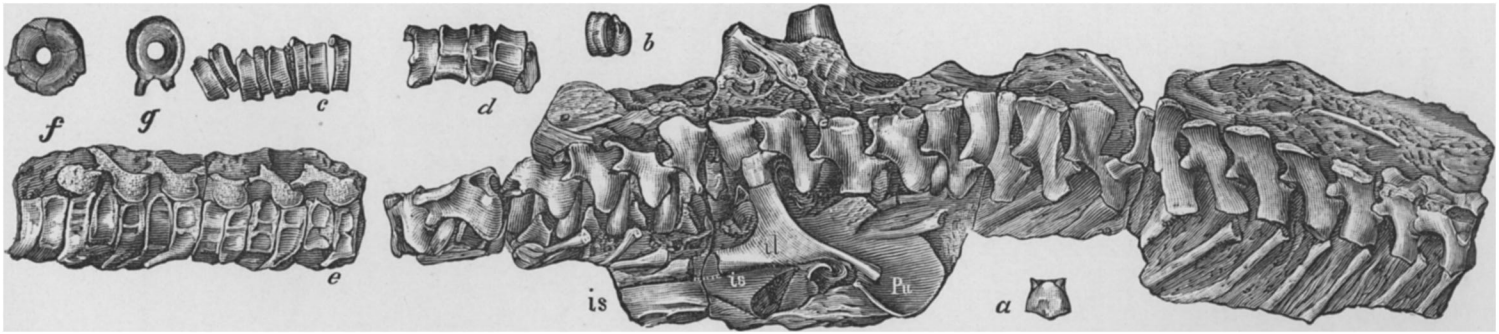
Two species are known, *Z. serratus* Cope, from Texas and *Z. apicalis* from New Mexico. In the latter the neural spines have much expanded apices, with sculptured superior surfaces. The animal may have been four or five feet in length, while the *Z. serratus* could not have exceeded three feet. Both species were well protected from the assaults of the cotemporary carnivorous saurians by their dermoössifications.

EMBOLOMERI.

I proposed this order in 1880[1] to receive the family of the Cricotidæ. This remarkable form has been characterized in this journal[2] and elsewhere, by the complete development of its centra and intercentra, both of which form entire vertebral bodies which in pairs support single neural arches. No such character has been detected in the known divisions of the Stegocephali. Its

[1] AMERICAN NATURALIST, p. 610.

[2] Loc. cit. 1876, p. 405; 1878. p. 319. Proceedings Am. Philos, Soc., 1878, 523.



1 CRICOTUS HETEROCLITUS Cope. $\frac{2}{3}$.

characters were given as follows. I have not been able to expose the occipital condyle in my specimens.

Centra and intercentra subequally developed as vertebral bodies, a single neural arch supported by one of each, forming a double body. Chevron bones supported only by intercentra. Basioccipital vertebral articulation connected with the first vertebra by an undivided discoid intercentrum.

Thus the peculiarity of the vertebral column in general is carried into the cephalic articulation, and we have, instead of the complex atlas of the Rachitomi, a single body connecting the occipital condyle and first vertebra. This body represents, in all probability, *the single occipital condyle of the reptilian skull.* This part, as is well known, remains cartilaginous in the lizard long after the basioccipital is ossified,[1] and is a distinct element. In the Urodele Batrachia it appears, according to Albrecht, as the odontoid process of the *atlas.* The structure of Cricotus shows that it is a connate intercentrum. We have thus removed the last difficulty in the way of the proposition that the Reptilia are derivative of the Batrachia, viz., the difference in the cranio-vertebral articulation. But the former have not been derived from the Labyrinthodontia, as has been suggested, nor from the Rachitomi, but from the Embolomeri. The order of Reptilia which stands next to it is, of course, the Pelycosauria of the same period, which presents so many Batrachian characters, including intercentra, as I have for the first time pointed out in the paper above quoted.[2]

Professor Gaudry has been inclined to regard the bones which I have called intercentra as the true centra. But in the Embolomeri we have evidence that the pleurocentra are the true centra, since they assume the larger bulk, and support the neural arch and costal articulation, the intercentrum becoming more and more subordinate as we advance from the caudal series forwards. Moreover, the intercentrum bears the chevron bones in the Rhachitomi, and the Embolomeri, as they do in the cotemporary Pelycosauria.

I add to the ordinal characters above given, that the three pectoral shields of the Stegocephali are present here also.

[1] See Parker On the development of the skull of the Lizard, Philosophical Transactions, London, 1879.

[2] Intercentra remain in the cervical and dorsal series of Hatteria, and there is one at least in the cervicals of the Pythonomorpha.

Besides Cricotus, Fritsch describes a genus from Bohemia under the name Diplovertebron, which I suspect to belong to the Embolomeri.

In the family Cricotidæ the chorda dorsalis is persistent and large. The vertebral centra and intercentra are perforated so as to resemble some kinds of discoidal beads. They form a characteristic feature among the Permian fossils. The abdomen is protected by scales arranged in chevrons. There is a parietal foramen, and the supratemporal bone has a free external border like the squamosal of the crocodile.

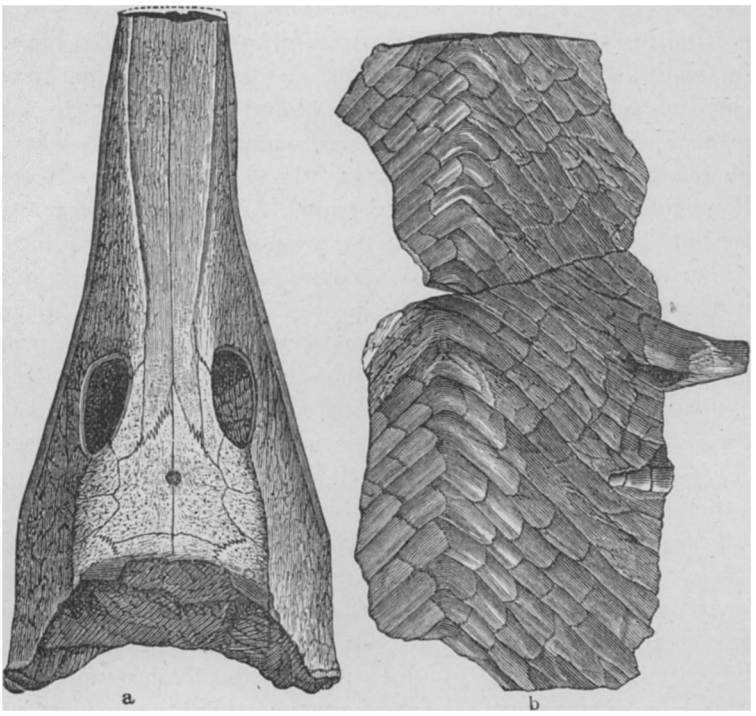


FIG. 7.—*Cricotus heteroclitus* Cope, the specimen figured on Plate v. Fig. *a*, skull from above, one-half nat. size, end of muzzle wanting; *b*, abdominal surface, showing scuta, distal extremity of femur and distal three phalanges of a digit, one-half nat. size.

CRICOTUS Cope.

In this genus the teeth are rather large, and are of subequal size in the external rows. The tail is long, and was apparently useful as a natatory organ. The terminal phalanges are obtuse as in salamanders, and without claws. The pelvis has the character of that of the Eryopidæ, but is less massive anteriorly. The

lower jaw has no posterior projecting angle. There are mucous grooves on the skull. The abdominal scales are oblong and in close contact with each other.

Cricotus heteroclitus was first found in Illinois, and afterwards in Texas. It is a more elongate animal than any of those described in the preceding pages, and it was furnished with short, rather stout limbs. It probably reached a length of ten feet, as my best preserved specimen, which is not the largest, measures about eight feet. It has an elongate triangular skull, eleven inches by six behind, with a singularly long, narrow, depressed muzzle, whose extremity overhangs the lower jaw completely. There are three pairs of mucous grooves; one is on each side of the roof of the muzzle, and runs out on the edge of the upper jaw, where it overhangs the extremity of the corresponding ramus. The second descends from behind the orbit, and running parallel to the edge of the upper jaw, joins the first at the usual position of a canine tooth in other forms. The third extends along the internal inferior edge of the mandibular ramus.

This species was probably aquatic in its habits. A smaller species, the *C. gibsoni*, has been described from Illinois. Its caudal vertebræ are of more elongate, cubical form than those of the *C. heteroclitus*.

EXPLANATION OF PLATES.

PLATE II.

Eryops megacephalus Cope, vertebral column, one-fourth natural size, the upper figure from the left side, the lower figure from below. The four sections of the column represented are parts of the same individual.

PLATE III.

Eryops megacephalus Cope, pelvic arch and femur, four-fifteenths natural size, belonging to the individual figured in Plate II. Figs. 11–14 pelvis; 11, left side; 12, front; 13, posterior view; 14, from below. Figs. 15–19, femur; 15, anterior view; 16, posterior view; 17, proximal view; 19, distal view.

PLATE IV.

Trimerorhachis insignis Cope, part of vertebral column flattened by pressure, of probably one individual, natural size. The upper figures (except *b*) from the right side; the lower (except *d*) from below. Figs. *a–d*, atlas and axis, the former with double intercentrum; the latter with single intercentrum. Fig. *b*, anterior view; Fig. *d*, posterior view.

PLATE V.

Cricotus heteroclitus Cope, part of skeleton of one individual, excepting Figs *f* and *g*, two-fifths natural size. The vertebræ on the larger block include the posterior extremity of the dorso-lumbar series of the specimen as preserved, viewed partly from above. Fig. *a*, first cervical intercentrum, anterior face; *b*, the same attached to front of first cervical centrum, lateral view; *c*, four cervical centra separated by intercentra, partly from below; *d*, *e*, caudal vertebræ from below; caudal vertebræ from right side. Figs. *f* and *g*, specimens of the same from Illinois, anterior views; *f*, a dorso-lumbar intercentrum; *g*, a caudal intercentrum with bases of chevron bone; all two-fifths natural size.